

Penguins use the two-voice system to recognize each other

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The sound-producing structure in birds is the syrinx, which is usually a two-part organ located at the junction of the bronchi. As each branch of the syrinx produces sound independently, many birds have two acoustic sources. Thirty years ago, we had anatomical, physiological and acoustical evidence of this two-voice phenomenon but no function was known. In songbirds, often these two voices with their respective harmonics are not activated simultaneously but they are obvious in large penguins and generate a beat pattern which varies between individuals. The emperor penguin breeds during the Antarctic winter, incubating and carrying its egg on its feet. Without the topographical cue of a nest, birds identify each other only by vocal means when switching duties during incubation or chick rearing. To test whether the two-voice system contains the identity code, we played back the modified call of their mate to both adults and also the modified call of their parents to chicks. Both the adults and the chicks replied to controls (two voices) but not to modified signals (one voice being experimentally suppressed). Our experiments demonstrate that the beat generated by the interaction of these two fundamental frequencies conveys information about individual identity and also propagates well through obstacles, being robust to sound degradation through the medium of bodies in a penguin colony. The two-voice structure is also clear in the call of other birds such as the king penguin, another non-nesting species, but not in the 14 other nesting penguins. We concluded that the two-voice phenomenon functions as an individual recognition system in species using few if any landmarks to meet. In penguins, this coding process, increasing the call complexity and resisting sound degradation, has evolved in parallel with the loss of territoriality.

Keywords: two-voice theory; vocal recognition; penguins

1. INTRODUCTION

When we consider the scientific literature on bird sound communication, we realize first that studies continue to focus on songbirds. We realize second that species-specific recognition has been intensively studied but that individual recognition is now increasingly investigated (Catchpole & Slater 1995; Bretagnolle 1996; Stoddard 1996) due to the fact that it (i) is widespread among birds (Dhont & Lambrecht 1992) and (ii) plays a major role in behavioural ecology through kin recognition (Beecher 1982).

In a seabird colony, the difficulty that partners experience in finding each other is extreme: their nests are dense and their feeding grounds are distant. Consequently, the study of acoustic individual recognition in colonial seabirds has produced papers such as those of Hutchinson *et al.* (1967), White & White (1970) and Beer (1979). The knowledge of topographical cues helps with the encounter, since the nest is used as a meeting point even when the chick becomes mobile (Penney 1968). The penguin family is particularly suitable for the study of acoustic identification because, first, it includes two non-nesting species (i.e. using few if any landmarks) and, second, experiments have demonstrated that penguins can identify their partner vocally but not visually (Jouventin 1982).

The genus *Aptenodytes* is unique in seabirds, comprising two large species which do not nest but which carry their single egg on their feet. The king penguin (*Aptenodytes pat-*

gonicus) breeds on flat beaches of sub-Antarctic islands and chicks waiting among several hundred others must identify the call of their parents against the louder background noise of the colony (described in humans as 'the cocktail party effect' by Cherry (1966) and now identified in king penguins by Aubin & Jouventin (1998); see also Lengagne *et al.* 1999, 2000). The only animal breeding during the harsh Antarctic winter, the emperor penguin (*Aptenodytes forsteri*), has no attachment zone and walks on the sea ice among several thousand breeders with its egg or young chick on its feet. To keep warm when temperatures drop down to -40°C and winds reach up to 300 km h^{-1} , brooders huddle at a density of ten birds per square metre (Prevost 1961). Being unable to use topographical cues and identify its partner visually, the emperor penguin seems the best acoustic model for studying individual recognition.

Its display call consists of a series of 'syllables' with a complex spectral structure (figure 1a) and is highly stereotyped within the individual and highly variable between individuals: the temporal pattern of syllables and silences allows individual recognition and sexing (Jouventin *et al.* 1979; Jouventin 1982). It can be compared with a barcode-containing identity if the syllabic structure is not degraded (Robisson *et al.* 1989). Bremond *et al.* (1990) analysed the possible parameters used for vocal recognition and pointed out another stereotyped feature: because the two syringeal structures are activated simultaneously, in contrast to many songbirds, the call of the emperor penguin comprises two simultaneous series of harmonically related bands of slightly different frequencies (figure 1b), i.e. a 'two-voice' signal.

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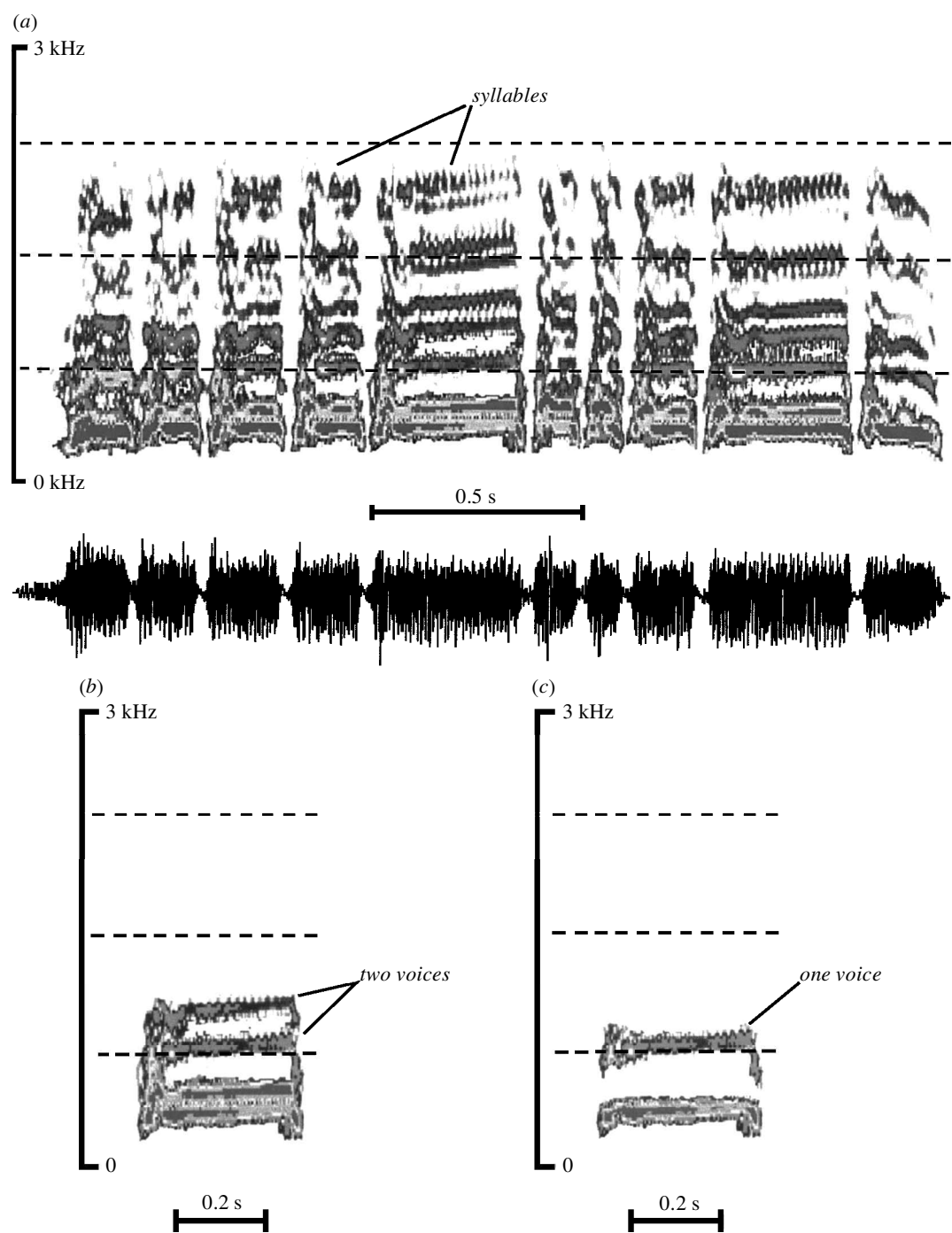


Figure 1. Sound spectrograms (1024 points window size, 16 Hz frequency resolution and 16 kHz sampling frequency) of (a) an emperor penguin display call used for playback (control) with oscillogram below, (b) one syllable of the low-pass filtered experimental call with only the fundamentals and first harmonics retained and (c) one syllable of the low-pass filtered experimental signal with one voice removed.

Unlike mammals, most birds are able to produce two voices simultaneously: their syrinx, which is usually a two-part organ, has an independent set of muscles and membranes involved in phonation and is controlled separately by the tracheosyringealis branches of the right and left hypoglossus nerves. The evidence for the two-voice phenomenon is anatomical (Stein 1968; Gaunt *et al.* 1982; Goller & Larsen 1997), physiological (Nottebohm & Nottebohm 1976; Nowicki & Capranica 1986; Suthers 1990) and acoustic (Greenewalt 1968; Beecher *et al.* 1985; Aubin 1986; Weisman *et al.* 1990). Some playback

experiments were performed in order to investigate the coding system by removing one of these two voices (Weary *et al.* 1986) but no function was found. In songbirds, this phenomenon is not obvious because either the two syringes are activated simultaneously, producing simple harmonic notes, or alternated to produce successive notes (Suthers 1990). However, for non-songbirds, these two acoustic sources generally generate two simultaneous fundamental frequencies and their respective harmonics. In the emperor penguin where the phenomenon is obvious, what is the function of this double-frequency

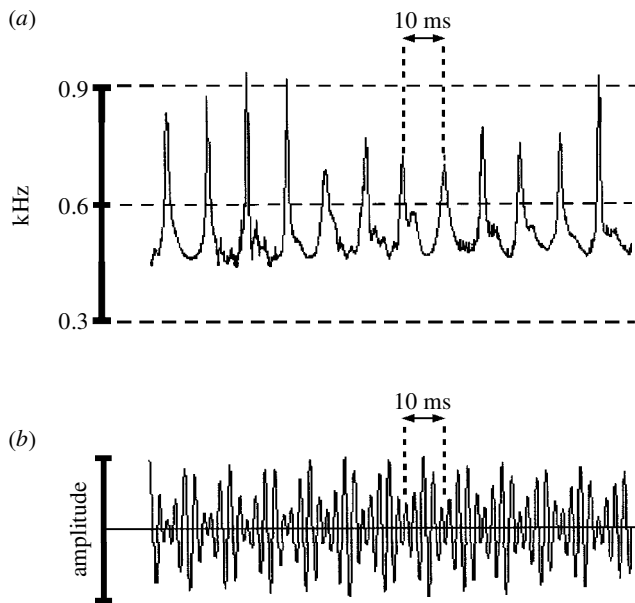


Figure 2. Emperor penguin display call: analysis of one natural syllable in the frequency and temporal domains. (a) The periodic frequency discontinuities coincide with (b) the periodic amplitude fluctuations and allow quantification of the period of the beat generated by the two acoustic sources (here a period duration of 10 ms, corresponding to a frequency of $1/0.01 = 100$ Hz).

structure, which was described by Greenewalt (1968) as 'the two-voice theory'?

2. METHODS

(a) Subjects and location

The recordings and experiments were carried out at the Pointe Géologie Archipelago ($66^{\circ}40'S$, $140^{\circ}01'E$), Terre Adélie, Antarctica, during the austral winter in 1997. Thirty-two adult emperor penguins were recorded and then their respective mates ($n=18$) or chicks ($n=16$) were marked on their chest or on a flipper (with a temporary plastic band) for identification.

(b) Recording and playback material

The display calls of emperor penguins were recorded with a Uher 4000C tape recorder (19 cm s^{-1} , frequency range 30–20 000 Hz (1 dB)) and an omnidirectional Sennheiser MKH 815T microphone (frequency response 100–20 000 Hz (1 dB)) mounted on a 3 m perch in order to approach the birds without disturbing them. The distance between the beak of the recorded bird and the microphone was *ca.* 1 m.

Experimental signals were broadcast with the previous tape recorder connected to a 50 W Audix PH3 self-powered loudspeaker (frequency response 100–5600 Hz (2 dB)). For the propagation tests, the signals were rerecorded by means of an omnidirectional Sennheiser MKH 815T microphone connected to a Sony TCD10 Pro II DAT (frequency response flat within the range 20–20 000 Hz).

(c) Sound synthesis and analysis

Analogue signals were digitized through a 16 bit Oros AU21 acquisition card (equipped with an anti-aliasing filter of 120 dB per octave) at a sampling rate of 16 kHz. They were stored on

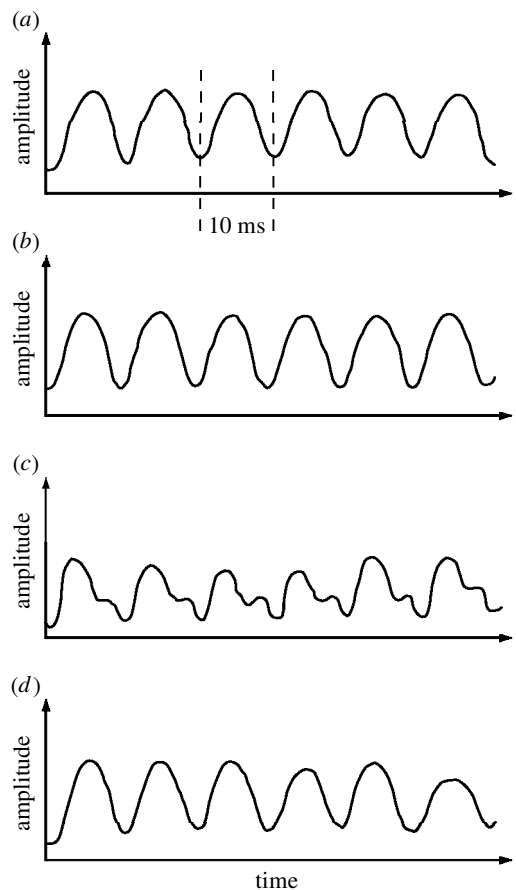


Figure 3. Envelopes of synthetic signals recorded at different distances from the loudspeaker. (a, b) At 1 m without intervening bodies. (a) True amplitude modulation and (b) amplitude modulation generated by beats of 350 and 450 Hz. (c, d) At 8 m after propagation through a penguin colony. (c) True amplitude modulation and (d) amplitude modulation generated by beats.

the hard disk of a computer and then analysed and modified with the Syntana analytical package (Aubin 1994).

The interaction of the two acoustic sources in each syllable generates a beat that is characterized by periodic fluctuations of the amplitude, the frequency of which equals the difference in the frequency of the two acoustic sources. To measure these beat values accurately, we used the Hilbert transform (Seggie 1987), which produced an instantaneous frequency. This method enabled us to follow the periodic frequency discontinuities which coincided with the periodic amplitude fluctuations (Bremond *et al.* 1990; Mbu-Nyamsi *et al.* 1994) and quantify precisely the period of the beat at which the frequency equals the difference in the frequency of the two acoustic sources (figure 2). In a previous study, Robisson *et al.* (1993) showed that this difference was highly stereotyped within the individual and variable between individuals.

(d) Playback experiments

We played back three sets of signals at 15 min intervals to marked adults during incubation and to marked chicks during rearing. Each set consisted of two identical signals separated by 3 s. One signal (control, figure 1a) corresponded to the natural display call of the mate of the adult tested or the parent of the chick. The two voices were difficult to distinguish and separate in upper harmonics: in the upper part of the spectrum, the

Table 1. Responses of adults and chicks to the playback of display calls (control), to the modified signal with two voices (low pass) and then to the tested signal (with a single voice)

(The vertical lines correspond to paired comparisons. *S*, observed value of the marginal homogeneity test (Agresti 1990) with Bonferroni-corrected, exact, one-sided *p*-values. The computations of the *p*-values were carried out using StatXact software (Cytel Software Corporation 1995).)

signals tested	no response	response	<i>n</i>	marginal homogeneity test
adults				
control	0	18	18	<i>S</i> = 2.00 and <i>p</i> = 0.25
low-pass, two voices	2	16	18	
low-pass, one voice	18	0	18	<i>S</i> = 16.00 and <i>p</i> < 0.01
chicks				
control	0	16	16	no discordant pair
low-pass, two voices	0	16	16	
low-pass, one voice	16	0	16	<i>S</i> = 16.00 and <i>p</i> < 0.01

corresponding harmonics generated by the two voices overlap and, consequently, our software was unable to separate them. For this reason, we also tested responses to a signal where only the fundamentals and the first harmonics of the control were kept (figure 1*b*), knowing that large penguins respond well to the playback of the lower half (Jouventin *et al.* 1999). Finally, we suppressed one of the two voices in the previous signal, the upper or lower in equal proportions for the different birds tested (figure 1*c*). Full removal of the upper harmonics or of one voice was done by applying optimal digital filtering (Press *et al.* 1988) with short-term overlapping (50%) fast Fourier transform (FFT) (4096 points window size, 4 Hz precision in frequency and 16 kHz sampling frequency). The temporal pattern of the natural call was preserved for all the experimental signals. It was described as a first system of vocal identification by Jouventin (1972, 1982) and tested by Robisson *et al.* (1989).

The order of presentation of the experimental signals was randomized for the different birds tested. The signals were played at a natural sound pressure level of *ca.* 95 dB (Robisson 1991) measured 1 m from the loudspeaker. The distance between the loudspeaker and the bird was *ca.* 7 m, which corresponds to the natural calling distance of an adult (Jouventin 1982; Robisson 1991). To evaluate the intensity of the response of the birds tested, we distinguished responses (calls in reply to the broadcast signal) and non-responses (no reaction).

(e) *Propagation experiments*

Experiments were carried out in order to analyse the modification of the two acoustic sources during propagation at different distances in the colony. Rather than directly using a natural call, we constructed synthetic signals (figure 3). The use of synthetic signals allowed us to exert tight control over the structure of the signal and, thus, take into account only the modifications of the parameters that we wanted to analyse for the propagation tests. On the basis of the analysis of natural syllables, we synthesized an amplitude modulation generated by the beats of two frequencies, the values of which corresponded to those of the two fundamental frequencies of a natural call. The values of these frequencies were *f*₁ = 350 Hz and *f*₂ = 450 Hz, with an amplitude ratio of 2 between the two

frequencies. For comparison purposes, we also synthesized the corresponding true amplitude modulation with a carrier frequency of 400 Hz, a modulation of 100 Hz and a modulation rate of 50%.

Both of these synthetic signals, which were of 5 s duration each, were broadcast in the centre of a colony with a normal density of birds (one bird per square metre) on a day without wind. A loudspeaker and microphone were mounted on a tripod at a height of 1 m (i.e. the height of an emperor penguin head) and positioned at distances of 1 m (reference), 8 m and 16 m. These relative positions of the speaker and microphone were chosen to simulate some acoustic adult–chick or male–female search situations inside a colony (Jouventin 1982; Robisson 1991). Propagation experiments were conducted under clear and dry weather conditions, with a wind speed of less 2 m s^{−1}.

3. RESULTS

(a) *Analysis of the beats in natural calls*

On the basis of the analysis of display calls of 43 individuals, we obtained a mean (± s.d.) value of the period of the beat of 65.2 Hz (± 14.1 Hz). According to a previous study (Robisson 1992), the mean frequency values of the fundamentals measured on 23 emperor penguins were 371 Hz for the lower voice (*f*₁) and 432 Hz for the upper voice (*f*₂). The mean value of the period of the beat, which was deduced from the difference *f*₂ − *f*₁, was 60 Hz. This value is very close to the one that we obtained with the instantaneous frequency measurement.

(b) *Playback experiments with one or two voices*

The results of the playback of (i) the control call, (ii) the lower frequency part of the call and (iii) the previous signal with one of the two voices suppressed are compared in table 1. All of the adults (*n* = 18) and chicks (*n* = 16) called in reply to the control signal. The lower frequency part of the call did not have as strong an effect on adults but induced a response in all but two of the individuals. Nevertheless, no significant difference was found between the responses obtained with this signal

Table 2. Mean (s.d.) period values of the amplitude modulation generated by the beats and the corresponding true amplitude modulation recorded at different distances

(Bravais–Pearson correlation coefficients between each of the 80 000 points of the envelope of the propagated signals (8 and 16 m) and the corresponding points of the reference signal (1 m) are also computed. ** $p < 0.01$.)

	1 m	8 m	16 m
beats			
mean \pm s.d. period duration (ms) ($n = 50$)	10.10 \pm 0.17	9.93 \pm 0.29	10.17 \pm 0.47
correlation for envelopes (reference 1 m)	—	0.86	0.78
amplitude modulation			
mean \pm s.d. period duration (ms) ($n = 50$)	10.00 \pm 0.15	9.75 \pm 0.91)	8.40 \pm 2.08
correlation for envelopes (reference 1 m)	—	0.55**	0.06**

and those obtained with the control signal. Concerning chicks, all individuals called in reply to the lower frequency part of the call and no significant difference was found with the control signal. When one voice was experimentally suppressed, no response was observed in adults or chicks: compared with the results obtained with the previous signal, the differences are highly significant ($p < 0.01$ in each case).

(c) Propagation of beats through the colony

The duration of the period of the synthetic beat was 10 ms (1/100 Hz) in our propagation experiment, a value frequently encountered in natural syllables of emperor penguins. After a propagation of 8 m through the colony, the amplitude modulation generated by beats (figure 3*b*) is slightly degraded (figure 3*d*) whereas the true amplitude modulation (figure 3*a*) is strongly modified (figure 3*c*). The mean period duration of both these amplitude modulations (50 periods measured in each case) is compared for the 1 m, 8 m and 16 m distances of propagation in table 2. It appears that, for the amplitude modulation generated by beats, the mean period duration is kept, even after a 16 m propagation. This is not the case for the true amplitude modulation: after propagation, the mean period value is modified, particularly at a distance of 16 m. In the same way, the s.d. values of the true amplitude modulation increase strongly as the distance of propagation increases.

If we now consider the amplitude functions (envelopes) of the two synthetic signals, modifications of the propagated signals are weak only for the amplitude modulation generated by beats compared with the recording at 1 m. Thus, the correlation between the true amplitude modulation envelope recorded at 1 m and the other propagated ones significantly decreases as the distance and obstacles due to bird bodies increases.

4. DISCUSSION

(a) The two-voice coding process

Why are the high frequencies of the call so incidental in individual recognition? Emperor penguin communication is constrained by the propagation conditions: high frequencies of its call cannot propagate more than a few metres particularly through the medium of penguin bodies (Robisson 1991). Low frequencies propagate much more effectively and, thus, are more reliable information channels for penguins.

How does the two-voice system of identification work? The syllables of the emperor penguin's call consist of two frequency bands with their respective harmonics. The interaction of these frequencies generates a beat, which Bremond *et al.* (1990) suggested conveys information about individual identity, the period of the beat being the same in different calls of a bird and different between birds (Robisson *et al.* 1993). From our first experiment, it appears the two voices are necessary in order to allow individual recognition of partners, mates or parents. To our knowledge, this is the first time that a coding process based upon a simultaneous two-voice system has been identified.

(b) A twin-pass system

The syllables (complex sounds with harmonic series) and silences of the call represent an amplitude modulation which makes it possible to locate the emitter and decode identity in the continuously noisy environment of the colony. This temporal pattern is a system of identification which has been described already (Jouventin *et al.* 1979; Jouventin 1982) and tested (Robisson *et al.* 1989) and it is complemented by another more sophisticated system: the two-voice system with a coding–decoding based upon the amplitude modulation beats or the double-frequency structure. The temporal pattern of syllables associated with the two-voice system creates the huge variety of vocal signatures necessary to distinguish between several thousand birds breeding without nests, i.e. with only vocal cues. This is in accordance with the model proposed by Schleidt (1976) where the number of features is a component of individual distinctiveness.

(c) Why two coding systems?

If the temporal pattern of the call associated with the syllabic structure allows identification, what is the specificity of the two-voice system? We suggest that the beat generated by the interaction of these two frequencies conveys a complementary code that confirms the temporal pattern due to the succession of syllables. The amplitude modulation produced by the beats is also more robust to sound degradation than true amplitude modulation. To demonstrate this, we performed the second experiment, which demonstrated that the two-voice system of identification is more efficient in transmitting an identity code than a true amplitude modulation, particularly through the medium of bodies in a penguin colony.

The fact that true amplitude modulation is strongly modified during propagation in a colony is not surprising

since it is well known that signals acquire irregular amplitude fluctuations after propagation through a turbulent atmosphere or in the presence of irregularly moving objects (Marten & Marler 1977; Wiley & Richard 1978) and these amplitude fluctuations mask the amplitude modulation details in a signal. In contrast, sharp amplitude variations due to the silence-syllable succession are more resistant during propagation and beats generated by two fundamentals low in frequency propagate well through the medium of penguins' bodies.

Our studies concerning the emperor penguin call indicate that the temporal patterning of the syllables and the beats generated by the two voices in each syllable are important parameters serving individual recognition. Such a syllabic structure of the signal, which is highly redundant, seems well adapted to communication in a noisy and obstructed environment. In addition, these two parameters correspond to a code of identification based upon a time analysis. In the classical work on psychoacoustics, time integration and frequency integration were considered as almost independent (Watson & Gengel 1969). Time analysis appears to be a fast process compared with a spectrum analysis (Pimonow 1962; Nordmark 1970; Green 1985). Consequently, the two combined acoustic codes of identification used by the emperor penguin are particularly accurate in distinguishing birds quickly and both codes are associated with the lack of topographical cues of these travelling, breeding penguins.

(d) *An adaptation to the lack of visual cues*

The emperor penguin has an extraordinary way of life, but the two-voice system of recognition is not limited to one species and should be researched elsewhere. Even in its family, the emperor penguin is not the only penguin to have the two-voice structure in its call. Robisson (1992) found the double-frequency structure in the king penguin, the other large species of the genus *Aptenodytes*, but not in the five other genera of penguins: we know that the king penguin is also a non-nesting species whereas the other 14 penguins are all nesting species. We suggest that the two-voice system of individual recognition found in the emperor penguin and which also exists in the king penguin (Lengagne *et al.* 2000) results from special use of the particular vocal apparatus of birds, which has permitted this genus to compensate for the loss of territoriality by a sophisticated acoustic adaptation.

This study was supported by the Institut Français pour la Recherche et la Technologie Polaires. We are grateful to Liz Brooks, Lance Barrett-Lennard, Duncan Martin-Holloway and two anonymous referees for comments and improvements of the English.

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